Ethology **110,** 793—805 (2004)

ISSN 0179–1613

Does the Flower Constancy of Bumble Bees Reflect Foraging Economics?

Robert J. Gegear & James D. Thomson

Department of Zoology, University of Toronto, Toronto, Canada

Abstract

We examined the effects of floral reward level and spatial arrangement on the propensity of bumble bees to exhibit flower constancy. In three separate experiments, we compared the flower constancy of bees on dimorphic arrays of blue and yellow flowers that differed either in reward concentration, reward volume, or inter-flower distance. Overall, flower choice patterns varied among bees, ranging from random selection to complete constancy. When flowers contained greater reward volumes and were spaced farther apart, bees showed less flower constancy and more moves to closely neighbouring flowers. Changes in reward concentration had no effect on flower constancy; however, more dilute rewards produced shorter flight times between flowers. In addition, there was a strong positive relationship between degree of flower constancy and net rate of energy gain when flowers were spaced farther apart, indicating that constant bees were more economic foragers than inconstant bees. Together, these results support the view that the flower constancy of pollinators reflects an economic foraging decision.

Correspondence: Robert J. Gegear, Department of Zoology, University of Toronto, Toronto, Canada M5S 3G5. E-mail: rjgegear@zoo.utoronto.ca

Introduction

Individual pollinators often specialize temporarily on one flower type while bypassing equally or more rewarding flower types in the process (Darwin 1876; Grant 1950; Waser 1986; Goulson & Wright 1998). This selective foraging, known as flower constancy, provides obvious fitness benefits to out-crossed flowering plants by limiting the transfer of pollen to conspecific plants (Waser 1983). However, why pollinators exhibit flower constancy remains unclear, despite an extensive literature during the past century (see, for reviews, Chittka et al. 1999; Goulson 1999).

The most widely accepted explanations for flower constancy invoke limited cognitive abilities of pollinators (Lewis 1986; Waser 1986; Goulson 2000;

U. S. Copyright Clearance Center Code Statement: 0179-1613/2004/11010–793/$15.00/0 www.blackwell-synergy.com

Gegear & Laverty 2001). Although the specific nature of these limitations is not clear, it is assumed that pollinators forage less economically when attempting to manage information about more than one flower type at a time. Therefore selecting a single type (constancy) minimizes the cost of alternating between flower types (random foraging). This view of flower constancy bears two implications. First, constancy involves a trade-off between the costs of alternating between flower types and the costs of specializing on a single flower type. Secondly, pollinators can assess the magnitude of these costs and decide whether constancy is the most economic foraging strategy for a given set of floral conditions.

Despite the general consensus that pollinator constancy is related to foraging economics, there are few clear demonstrations. Several studies report that pollinators experience a cost when switching between different flower types (Lewis 1986; Laverty 1994b; Dukas 1995; Gegear & Laverty 1995; Chittka & Thomson 1997); however, these costs were either too small to compensate for the increased travel times between flowers required by constancy (Gegear & Laverty 1995; Goulson et al. 1997) or they did not correspond to an increase in flower constancy (Gegear & Laverty 1998). The propensity of pollinators to move between similar flower types has been correlated with decreased flight duration (Marden & Waddington 1981; Keasar et al. 1996; Chittka et al. 1997; Goulson et al. 1997), which suggests that flower constancy is influenced by travel costs. However, the direct effects of reward level and spatial distribution on flower constancy have rarely been considered under controlled conditions. Clearly, such studies are required before flower constancy in pollinators can be considered an economic foraging strategy.

Here we use a novel experimental approach to examine the traditional view that flower constancy reflects foraging economics. Instead of attempting to establish the specific cognitive limitation responsible for increased switching or perceptual costs, as has been the focus of most previous studies of constancy (e.g. Lewis 1986; Gegear & Laverty 1995, 1998; Goulson et al. 1997; Hill et al. 1997; Goulson 2000), our experiments assess whether changes in the cost of bypassing rewarding flower types affects constancy. We measured and compared the flower constancy exhibited by bumble bees (*Bombus impatiens* Cresson) visiting arrays of blue and yellow artificial flowers differing either in reward volume, reward concentration, or inter-flower distance. We used yellow and blue flowers because this contrast has previously been associated with switching costs (Dukas 1995), and invokes strong flower constancy in honey bees under some conditions (Hill et al. 1997, 2001). We expect that if constancy reflects an economic foraging strategy, bees will be more constant when flowers offer a lower reward or are spaced closer together, because of the lower relative cost of bypassing flowers in the former situations. We also examine whether flower constancy is an economic foraging strategy by relating the net rate of energy gain (J/s) of bees to their respective flower constancy.

Materials and Methods

Bees

Bumble bee (*B. impatiens*) colonies were obtained from Biobest Biological Systems Canada (Leamington, ON, Canada). Colonies were connected to a screened enclosure (1.5 m long × 1.05 m wide × 1 m high) with a tunnel constructed from wire mesh. The tunnel was gated so that we could control the entry of bees into the enclosure. A door (0.4 m × 0.4 m) located on one side of the enclosure allowed the experimenter access inside. Colonies had a constant supply of pollen and were supplemented with 30% sucrose solution (w/w) while not being tested. A minimum of two colonies was used per experimental treatment. Bees (and colonies) were tested only once; thus, groups of test bees were independent between experiments and treatments within an experiment.

Artificial Flowers and Arrays used in Experiments

Artificial flower types (hereafter referred to as 'flowers') were modelled after those used by Gegear & Laverty (1998) and simulated the natural open-tubed flowers discussed by Laverty (1994a)). We constructed each flower by removing the cap from a 1.5 ml Eppendorf centrifuge tube (either blue or yellow) and then fastening a 3-cm circular 'corolla' around the entrance of the centrifuge tube. The corolla was constructed from either yellow or blue acetate and matched the spectral reflectance. To access each flower, bees had to land on the corolla and crawl to the bottom of the tube to obtain sucrose solution that had been added previously with a Hamilton PB 600-1 microdispenser (Reno, NV, USA).

We used an array design that allowed us to control the distribution, spacing, and abundance of flowers. A total of 60 flowers were embedded 1 cm into a 3.5-cm Styrofoam block (1.4 m × 1 m) covered in green construction paper. The green background was replaced either after every day that experiments were conducted or upon being soiled by foraging bees. Flowers were placed in 10 rows of six with adjacent rows offset by half the distance between flowers in each row. On mixed arrays, we spaced 30 blue and 30 yellow flowers in alternating rows of two, so that bees always had an equal choice of both colours (both nearest and second-nearest neighbours) upon leaving any flower (Fig. 1).

Experimental Procedure

We conducted three experiments to assess the effect of reward volume, reward concentration, and inter-flower distance on the constancy of bees. For each experiment, we ran two treatments that were identical except for the floral characteristic under consideration. Table 1 lists the floral characteristics that were used in each experimental treatment. The following procedure, which was based on the procedure used by Gegear & Laverty (1998), was used for all three experiments.

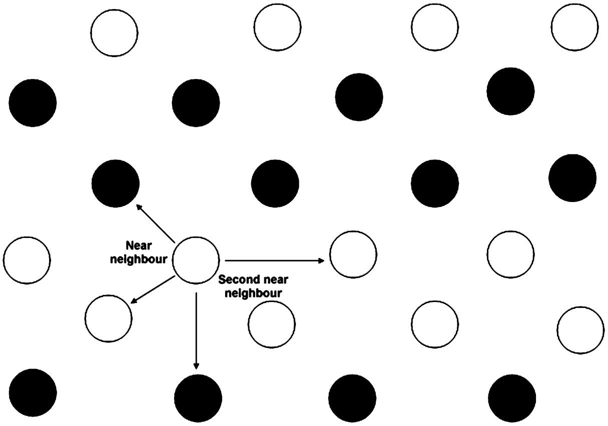

Fig. 1: Design of the colour dimorphic floral array used in experiments. Flowers were placed in 10 rows of six such that adjacent rows were offset by half the distance between flowers in each row. The flight distance from any flower to each of the near and second-near neighbours was 7 cm and 10 cm in expts 1–3a and 15 cm and 22 cm in expt 3b, respectively. We distributed 30 blue and 30 yellow flowers in alternating rows of two, so that bees always had an equal choice of both colours (both near and second-near neighbours) upon leaving any flower. Filled and open circles represent blue and yellow flowers, respectively

Training to flowers

We trained bees to each flower colour prior to testing to ensure that they had both learned to handle the artificial flowers and associated each colour with a reward. Flowers provided the same concentrations of sucrose as they had during the subsequent testing phase (see Table 1) and were re-filled immediately after being drained so that bees did not experience any empty flowers while foraging. To train bees, we allowed them to forage consecutively on monotypic (pure) arrays of each colour for 2 h per array. During training, we allowed multiple bees onto the arrays simultaneously; however, individuals were monitored to make

Table 1: Summary of floral characteristics that were used to assess the effects of volume (expt 1), concentration (expt 2) of sucrose reward, and inter-flower distance (expt 3) on the flower constancy of bumble bees

Experiment	n	Volume (μl)	Concentration (% sucrose)	Distance (cm)
1a	11	2	30	7
1b	11	10	30	7
2a	15	2	10	7
2b	10	2	45	7
3a	11	2	30	7
3b	11	2	30	15

n, the total number of bees used per treatment.

sure that they continued to forage during the 2 h. To identify bees during testing, we marked the thorax and/or abdomen using various combinations of coloured correction fluid. After the bees had been trained to both colours, they were returned to the colony for testing.

Testing

The day after training, we tested a single experienced bee by allowing it to visit pure arrays of each colour for three foraging trips (approx. 90 flower visits) per array. This procedure was used to control for the possibility that bees had not retained either the handling method of the flower or the colour–reward association overnight. To control for the possible effect of colour order on the subsequent flower choice of bees on the mixed array, half of the bees tested visited yellow flowers first followed by blue flowers and the other half of the test bees received the opposite order. We then presented the bee with a mixed array of both colours and videotaped the first 70 flower visits for later analysis of the visit sequence. During testing, flowers always contained the same volume and concentration of sucrose reward (Table 1) and we re-filled drained flowers so that bees always encountered the same number of rewarding flowers while foraging. To assure that individuals were not disturbed while foraging, re-filling occurred as the test bee entered a subsequent flower. Flowers were replaced between test bees.

Variables Measured

Based on the recorded visit sequence of each bee, we measured flower constancy, mean inter-flower flight time, proportion of visits to a close flower, and net rate of energy gain. Flower constancy is defined as the tendency to visit one flower type sequentially while bypassing other equally or more rewarding flower types (Waser 1986). In the past, Bateman's Index (Bateman 1951) has been used to quantify flower constancy (e.g. Waser 1983, 1986); however, Bateman's Index has one significant problem: it is undefined as to when individuals exclusively visit one flower type (Chittka et al. 2001). To circumvent this problem, we used the following measure of constancy adapted from Jacobs (1974): Constancy Index, $CI = (c - e)/(c + e - 2ce)$, where 'c' is the proportion of moves between the same colour, and 'e' the proportion of moves between the same colour expected based on the overall frequency of each colour selected in a given experiment. Thus, CI represents the degree to which an individual moved between flowers of the same colour, controlling for any bias in the frequency of visits to each colour shown by all bees tested in the treatment. Possible values range from -1 (complete inconstancy) to 0 (random foraging) to $+1$ (complete constancy).

To determine inter-flower flight time, we first timed a set of 10 consecutive flower visits from the middle of the flower visit sequence. We started timing when the bee landed on the first flower and stopped timing when the bee departed from the 10th flower. We then subtracted the time spent on each of the

10 flowers from the total time over the 10 visits. Finally, we divided the total flight time by the number of inter-flower transitions to convert values to mean inter-flower flight time per flower transition. Thus, inter-flower flight time is the time between when a bee left one flower and landed on the next flower. We determined the proportion of visits to a close flower by dividing the total number of moves between near-neighbour flowers (Fig. 1) by the total number of flower transitions.

We estimated each bee's net rate of energy gain (NREG) (J/s) = $[(nEpVC) - M(T_pK_p + T_fK_f)]/[T_p + T_f]$ (adapted from Harder 1988), where 'n' is the number of flowers visits observed, 'E' the energy content of 1 mg of sucrose (15.5 J; Heinrich 1975), 'p' the density of the sugar (mg/μl), 'V' the volume of nectar taken per flower (μl), 'C' the concentration of nectar (%), 'M' the mass of bee (g), T_p and T_f are the total amount of time spent probing and flying during n flower visits (s), respectively and K_p and K_f are the energetic costs of probing (0.034 J/g/s; Pyke 1978) and flying (0.435 J/g/s; Heinrich 1975), respectively.

To test whether changes in the cost to bypass an encountered flower influenced the flower constancy of bees, we used a Student's t-test to compare CI when flowers differed in reward volume (expt 1a and b), reward concentration (expt 2a and b) and inter-flower distance (expt 3a and b). We also tested for more general changes in the movement patterns of bees in response to changes in the cost of bypassing encountered flowers by comparing inter-flower flight times and proportion of visits to a close flower between treatments in each experiment. We analysed flight time data using Student's t-tests and proportion data using a logistic regression, treating the proportion of near-moves as the binary dependent variable and experimental treatment as a categorical explanatory variable.

We next determined whether more constant bees were more economic foragers by using a correlation analysis to test the relationship between CI and NREG within each treatment. Finally, we tested for relationships between CI and inter-flower flight time and proportion of visits to a close flower in each treatment using correlation analysis. The probability values obtained were corrected for multiple tests using a sequential Bonferroni test (Rice 1989).

Results

Across experiments, flower constancy varied widely among bees (Table 2). CI ranged from −0.05 to 1, indicating that some bees moved randomly between colours, whereas other bees foraged solely on one colour. Most bees (52 of 68 tested) showed moderate to high levels of constancy (CI = 0.4–1); however, there was no overall bias in the observed number of visits to yellow and blue flowers [2402 of 4760 (51%) visits to blue flowers vs. 2358 of 4760 (49%) visits to yellow flowers; one-sample t-test (two-tailed), $p > 0.05$], indicating that the observed constancy was not because bees, as a group, preferred flowers of one colour.

Table 2: Constancy Index (CI) of each bee tested in expts 1–3 (n = 68). Possible values range from −1 (complete inconstancy) to 0 (random foraging) to +1 (complete constancy)

Bee	Expt 1		Expt 2		Expt 3	
	2 μl	10 μl	10%	45%	7 cm	15 cm
1	0.67	0.09	0.88	0.35	0.50	0.35
2	0.94	0.12	1	0.38	1	0.35
3	1	0.06	1	1	0.46	0.53
4	1	1	1	0.59	0.15	0.21
5	0.52	−0.05	0.79	0.59	1	0.24
6	0.17	0.56	0.19	0.94	1	0.47
7	0.79	0.53	0.63	1	1	−0.02
8	0.85	0.76	1	0.59	1	0.30
9	0.73	1	0.94	1	0.42	0.01
10	0.94	1	0.69	0.91	0.33	0.38
11	0.82	0.55	1		0.16	
12			0.63			
13			0.45			
14			1			
15			0.94			

Experiment 1: Nectar Volume

Bees visiting flowers with 10 μl of reward were less constant than bees visiting flowers with 2 μl of reward (Fig. 2a; $t_{20} = -1.79$, $p = 0.04$). In addition, bees visited a close flower more often when flowers had 10 μl of reward than when flowers had 2 μl reward (Fig. 2b; $\chi^2 = 13.45$, $p = 0.0002$). Despite the fact that bees visited close neighbours more often when flowers had greater reward volume, the amount of time between consecutive flower visits did not differ significantly between treatments ($t_{20} = 0.503$, $p = 0.31$). There were no significant correlations between CI and NREG, mean inter-flower flight time, or proportion of visits to a close flower at either reward volume.

Experiment 2: Nectar Concentration

The flower constancy of bees was not affected by variation in the reward concentration of available flowers (Fig. 2a; $t_{23} = -0.790$, $p = 0.22$). Bees took longer time during consecutive flower visits when visiting flowers with a higher sucrose concentration than those visiting flowers with a lower sucrose concentration (Fig. 2c; $t_{23} = 2.84$, $p = 0.004$), but the propensity of bees to visit a close flower did not differ between reward concentrations ($\chi^2 = 0.03$, $p = 0.85$). Flower constancy did not vary significantly with NREG, inter-flower flight time, or proportion of visits to a close flower at either reward concentration. However, there was a weak tendency for more constant bees to visit closer flowers when nectar was more dilute ($r_{15} = -0.47$, $p = 0.08$).

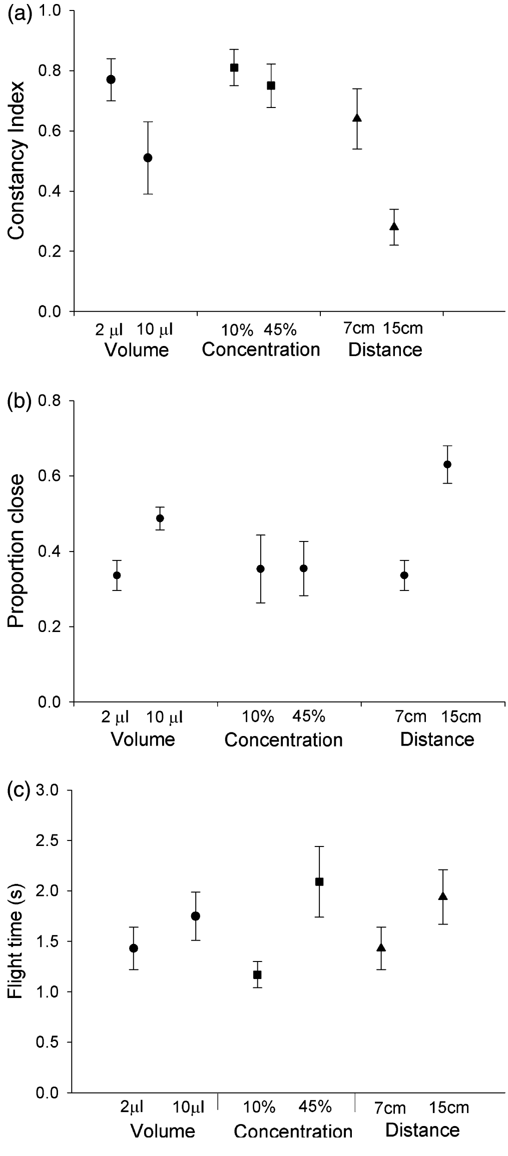

Fig. 2: (a) Constancy Index (CI), (b) proportion of visits to a close flower, and (c) inter-flower flight time (in seconds) of bees in response to varying reward volume (expt 1a and b; n = 22), reward concentration (expt 2a and b; n = 25), and inter-flower distance (expt 3a and b; n = 21). Possible values range from −1 (complete inconstancy) to 0 (random foraging) to +1 (complete constancy). Inter-flower flight times represent the average time (in seconds) between two consecutive flower visits (departing the first until landing on the second) computed over 10 successive visits. Values are in mean ± SE (see Table 1 for the floral properties used in each experimental condition)

Experiment 3: Flower Spacing

Bees visiting flowers that were spaced farther apart were less constant than bees visiting flowers that were spaced closer together (Fig. 2a; $t_{19} = -2.79$, $p = 0.006$). Bees also visited a close flower more often when flowers were spaced farther apart than when flowers were spaced closer together (Fig. 2b; $\chi^2 = 80.59$, $p < 0.0001$). There was a tendency for bees to have longer inter-flower flight times when flowers were spaced farther apart; however, this difference was not significant (Fig. 2c; $t_{19} = 1.52$, $p = 0.07$).

When flowers were spaced 15 cm apart, more constant bees were more economic foragers than less constant bees (Fig. 3a; $r_{10} = 0.70$, $p = 0.02$). In addition, CI varied positively with the proportion of visits to a close flower (Fig. 3b; $r_{10} = 0.64$, $p = 0.04$), and negatively with inter-flower flight time when inter-flower distance was 15 cm (Fig. 3c; $r_{10} = -0.74$, $p = 0.01$), indicating that more constant bees had shorter inter-flower flight durations and infrequently bypassed encountered flowers. In contrast, CI did not vary with either the proportion of visits to a close flower or inter-flower flight distance when flowers were spaced 7 cm apart. CI tended to vary positively with NREG at the closer inter-flower distance ($r_{15} = 0.54$, $p = 0.08$), indicating that there was a tendency for more constant bees to accumulate energy faster than less constant bees; however, the correlation was not significant.

Discussion

Although flower constancy has been described in many pollinator taxa, its cause remains unclear. Our study tested the hypothesis that the flower constancy of pollinators reflects an economic foraging decision by varying the cost to bypass an encountered flower. If constancy reflects foraging economics, then it should be reduced when available flowers have greater nectar levels (volumes or concentrations) or are spaced farther apart because of the greater cost to bypass an encountered flower. As predicted, bees were more constant at a smaller nectar volume and shorter inter-flower distance than at a larger nectar volume and longer inter-flower distance. Although bees tended to be less constant when nectar was more concentrated, this effect was not significant. As bees are sensitive to changes in the concentration of floral reward (Wiegmann et al. 2003), this contrast could have resulted because of differences in the response of bumble bees to variation in nectar volume and nectar concentration. Interestingly, when the overall energy content of nectar per flower at the same inter-flower distance (7 cm) is considered (expts 1–3a), there was a tendency for constancy to decrease with increases in the energy content of nectar (Fig. 2; energy content per flower: expt 1b > expt 2b > expts 1a and 3a > expt 2a), suggesting that the energy content of flowers may be a better indicator of the cost to bypass an encountered flower than nectar volume or concentration.

Previous studies have found that bumble bees tend to be more constant when inter-flower distances or flight times are short, and have suggested that these

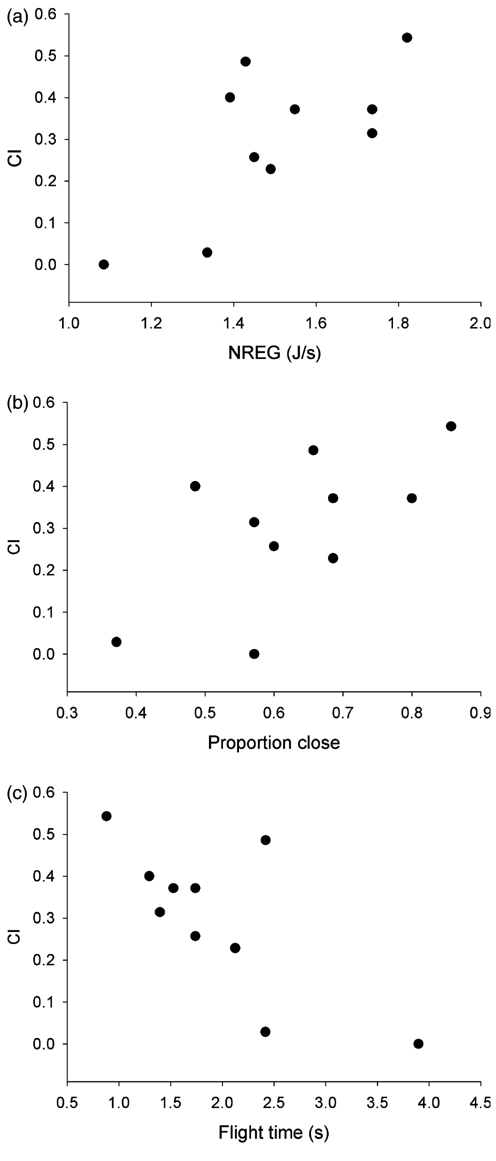

Fig. 3: Constancy Index (CI) values vs. (a) net rate of energy gain (NREG), (b) proportion of moves to a close neighbouring flower, and (c) mean inter-flower flight time of bees when flowers were spaced 15 cm apart (expt 3b; n = 10)

relationships are pre-programmed components of bee foraging (e.g. Keasar et al. 1996; Chittka et al. 1997). In our experiments, bees visited close flowers more frequently when reward volume was large and flowers were spaced far apart and had increased flight times when nectar was concentrated. However, there was a negative relationship between the flower constancy and flight time of bees only when flowers were widely spaced. In fact, bees tended to fly shorter distances and were less constant when reward volume was large (expt 1). Together, these results provide little support for pre-programmed relationships between flower constancy and either flight time or flight distance. Rather, our data are more consistent with constancy and other movement rules, such as area restricted search (Motro & Schmida 1995), being separate decision processes, which may be correlated in some foraging environments. Moreover, our results are consistent with each type of movement pattern being largely based on foraging economics. Increased flight distances after bees encounter small nectar volumes is an economic foraging strategy based on area-restricted search (Heinrich 1979; Motro & Schmida 1995; Keasar et al. 1996). Independently, flower constancy is an economic foraging strategy when familiar flowers have smaller nectar volumes or are spaced closer together based on the cost to bypass an encountered flower.

As a consequence of its dependence on nectar volume and the spatial arrangement of flowers, flower constancy should also be related to energetic returns if it is the best strategy for a given set of floral conditions. Constancy varied positively with a bee's net rate of energy gain when inter-flower distance was 15 cm, but not for any other experimental condition; however, there was a weak but insignificant positive relationship between constancy and NREG when inter-flower distance was 7 cm. Because constant bees in the far inter-flower distance treatment also visited closer flowers and had shorter flight times than less constant bees, it is not surprising that more constant bees were more economic foragers. It is unclear, however, why bees visiting close flowers would continue to select the same colour when the alternate colour was also available at the same distance. Perhaps bees that repeatedly visited flowers of the same colour saved time because they were better able to detect and/or process colour information. This interpretation is consistent with reports that bumble bees are limited in their ability to detect and process multiple colours at the same time (Dukas 1995; Gumbert 2000; Spaethe et al. 2001), but additional studies examining the search efficiency of constant and inconstant bees at varying inter-flower distances would be beneficial.

Pollinator flower constancy remains enigmatic because the benefit of bypassing equally or more rewarding flowers in favour of a single flower type has proven difficult to ascertain. Indeed, bees in most experimental treatments tended to exhibit some degree of flower constancy although there was no apparent economic incentive to do so. For the most part, previous studies of pollinator constancy have tested hypotheses related to the specific cost of visiting more than one flower type at the same time (Lewis 1986; Laverty 1994b; Goulson et al. 1997; Gegear & Laverty 2001). Our results suggest that flower constancy would be understood more completely by also considering the cost to bypass an encountered flower for a given set of floral conditions. For example, the extent of the limitation on the ability of pollinators to manage multiple floral cues at the same time (i.e. differences in the colour, odour, size, and/or shape of flowers) could be assessed indirectly by measuring the constancy of individuals at varying reward levels and/or inter-flower distances. Results of such experiments should provide valuable insight into the factors governing the foraging decisions of pollinators, and will enhance our understanding of the relationship between floral diversity and pollinator behaviour.

Acknowledgements

We thank S. Colla and A. Puentez for their assistance with data collection. This work was supported by a grant to J.D. Thomson from the Natural Sciences and Engineering Research Council of Canada, and an NSERC post-doctoral fellowship awarded to R.J. Gegear.

Literature Cited

Bateman, A. J. 1951: The taxonomic discrimination of bees. Heredity **5,** 271—278.

Chittka, L. & Thomson, J. D. 1997: Sensory-motor learning and its relevance for task specialization in bumble bees. Behav. Ecol. Sociobiol. **41,** 385—398.

Chittka, L., Gumbert, A. & Kunze, J. 1997: Foraging dynamics of bumble bees: correlates of movements within and between plant species. Behav. Ecol. **8,** 239—249.

Chittka, L., Thomson, J. D. & Waser, N. M. 1999: Flower constancy, insect psychology, and plant evolution. Naturwissenschaften **86,** 361—377.

Chittka, L., Spaethe, J., Schmidt, A. & Hickelsberger, A. 2001: Adaptation, constraint and chance in the evolution of flower color and pollinator color vision. In: Cognitive Ecology of Pollination: Animal Behaviour and Floral Evolution (Chittka, L. & Thomson, J. D., eds). Cambridge Univ. Press, Cambridge, pp. 106—126.

Darwin, C. 1876: On the Effects of Cross and Self Fertilization in the Vegetable Kingdom. John Murray, London.

Dukas, R. 1995: Transfer and interference in bumble bee learning. Anim. Behav. **49,** 1481—1490.

Gegear, R. J. & Laverty, T. M. 1995: Effect of flower complexity on relearning flower handling skills in bumble bees. Can. J. Zool. **73,** 2052—2058.

Gegear, R. J. & Laverty, T. M. 1998: How many flower types can bumble bees forage on at the same time. Can. J. Zool. **76,** 1358—1365.

Gegear, R. J. & Laverty, T. M. 2001: The effect of variation among floral traits on the flower constancy of pollinators. In: Cognitive Ecology of Pollination: Animal Behaviour and Floral Evolution (Chittka, L. & Thomson, J. D., eds). Cambridge Univ. Press, Cambridge, pp. 1—20.

Goulson, D. 1999: Forager strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. Perspect. Plant Ecol. Evol. Systemat. **2,** 185—209.

Goulson, D. 2000: Are insects flower constant because they use search images to find flowers? Oikos **88,** 547—552.

Goulson, D. & Wright, N. P. 1998: Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). Behav. Ecol. **9,** 213—219.

Goulson, D., Stout, J. C. & Hawson, S. A. 1997: Can flower constancy in nectaring butterflies be explained by Darwin's interference hypothesis? Oecologia **112,** 225—231.

Grant, V. 1950: The flower constancy of bees. Bot. Rev. **16,** 379—398.

Gumbert, A. 2000: Color choices by bumble bees (*Bombus terrestris*): innate preferences and generalization after learning. Behav. Ecol. Sociobiol. **48,** 36—43.

Harder, L. D. 1988: Choice of individual flowers by bumble bees: interaction of morphology, time and energy. Behaviour **104,** 60—77.

Heinrich, B. 1975: Thermoregulation in bumblebees 2. Energetics of warm-up and free-flight. J. Compar. Physiol. **96,** 155—166.

Heinrich, B. 1979: 'Majoring' and 'minoring' by foraging bumblebees, *Bombus vegans*: an experimental analysis. Ecology **60,** 245—255.

Hill, P. S. M., Wells, P. H. & Wells, H. 1997: Spontaneous flower constancy and learning in honey bees as a function of color. Anim. Behav. **54,** 615—627.

Hill, P. S. M., Hollis, J. & Wells, H. 2001: Foraging decisions in nectivores: unexpected interactions between flower constancy and energetic rewards. Anim. Behav. **62,** 729—737.

Jacobs, J. 1974: Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's Electivity Index. Oecologia **14,** 413—417.

Keasar, T., Shmida, A. & Motro, U. 1996: Innate movement rules in foraging bees: Flight distances are affected by recent rewards and are correlated with choice of flower type. Behav. Ecol. Sociobiol. **39,** 381—388.

Laverty, T. M. 1994a: Bumble bee learning and flower morphology. Anim. Behav. **47,** 531—545.

Laverty, T. M. 1994b: Costs to foraging bumble bees to switching plant species. Can. J. Zool. **72,** 43—47.

Lewis, A. C. 1986: Memory constraints and flower choice in *Pieris rapae*. Science **232,** 863—865.

Marden, J. H. & Waddington, K. D. 1981: Floral choices by honeybees in relation to the relative distances to flowers. Physiol. Entomol. **6,** 431—435.

Motro, U. & Schmida, A. 1995: Near-far search: an evolutionarily stable foraging strategy. J. Theor. Biol. **173,** 15—22.

Pyke, G. H. 1978: Optimal body size in bumble bees. Oecologia **34,** 255—266.

Rice, W. R. 1989: Analyzing tables of statistical tests. Evolution **43,** 223—225.

Spaethe, J., Tautz, J. & Chittka, L. 2001: Visual constraints in foraging bumble bees: flower size and color affect search time and flight behavior. Proc. Natl Acad. Sci. **98,** 3898—3903.

Waser, N. M. 1983: The adaptive nature of flower traits: ideas and evidence. In: Pollination Biology (Real, L. A., ed.). Academic Press, Orlando, FL, pp. 241—285.

Waser, N. M. 1986: Flower constancy: definition, cause and measurement. Am. Nat. **127,** 593—603.

Wiegmann, D. D., Wiegmann, D. A. & Waldron, F. A. 2003: Effects of a reward downshift on the consummatory behavior and flower choices of bumble bee foragers. Physiol. Behav. **79,** 561—566.

Received: February 14, 2004

Initial acceptance: April 19, 2004

Final acceptance: June 17, 2004 (S. K. Sakaluk)